The larval and post-larval development of the brachyuran crab *Geryon tridens* Kröyer (Family Geryonidae) reared in the laboratory

R. W. Ingle

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

Four zoeal stages, a megalopal and first crab stage of the N.E. Atlantic crab *Geryon tridens* are described from laboratory reared material and compared with the corresponding stages of the N.W. Atlantic *G. quinquedens*. Diagnostic features are given for distinguishing the zoeae and megalopa of *G. tridens* from those of the portunid crabs and from *Goneplax rhomboides* occurring in British waters. The juvenile crab stages of *G. tridens* are compared with those of the southern Atlantic deep water *G. longipes*. The developmental stages of *G. tridens* suggest that *Geryon* evolved from the same phylogenetic stock as the Portunidae, Xanthidae and perhaps a part of the Goneplacidae.

Introduction

The crab *Geryon tridens* Kröyer has been recorded from the waters of northern Scandinavia, the northern North Sea and the N.E. Atlantic Ocean to just south of Ireland (Christiansen, 1969 : 85–86 and BM (NH) records). Further southward its distribution is uncertain as some authorities (Bouvier, 1940 : 269) have synonymized *G. tridens* with the southern *G. longipes* A. Milne Edwards, while Zariquiey Alvarez (1968 : 389) has maintained *G. longipes* as a valid species.

Only the pre-zoea and first zoea of *G. tridens* have been described previously from laboratory hatched specimens of a female collected south of Bergen, Norway (Brattegard & Sankarankutty, 1967). In April 1975 an ovigerous *G. tridens* was trawled in the North Sea and presented to the BM(NH) by Dr M. S. Rolfe. The hatched larvae were successfully reared to provide material for the following description of the complete larval development of this species.

Materials and Methods

The ovigerous specimen was taken in the Auk oil field region, about 150 miles off the Firth of Forth, between 56°20·1′ N : 02°07′ W and 56°24·0′ N : 02°04′ W, in an 8 m beam trawl worked at 85 m from the MAFF R.V. *Corella*. The female and reared material are deposited in the Collections of the Zoology Department, BM(NH), reg. nos 1976 : 4; 1978 : 176–189.

The larvae were reared using the methods described by Rice & Ingle (1975 : 104) and Ingle & Clark (1977). All material was fixed and stored in the preservative formulated by Steedman (1976 : 148) until studies had been completed and then transferred to 70% ethanol for permanent storage. Drawings and measurements were made with the aid of a *camera lucida* and some morphological details were confirmed by scanning electron microscopy. Measurements taken were:

(a) the distance between tips of dorsal and rostral spines (T.T.), (b) carapace length from between the eyes to the posterio-lateral carapace margin (C.L.).

Results

Hatching occurred between 5 and 6 May 1975; an average of 69 days elapsed between hatching and the appearance of first crab stages. A percentage of the hatch reached seventh and one

Bull. Br. Mus. nat. Hist. (Zool.) **36** (4) : 217–232 Issued 25 October 1979

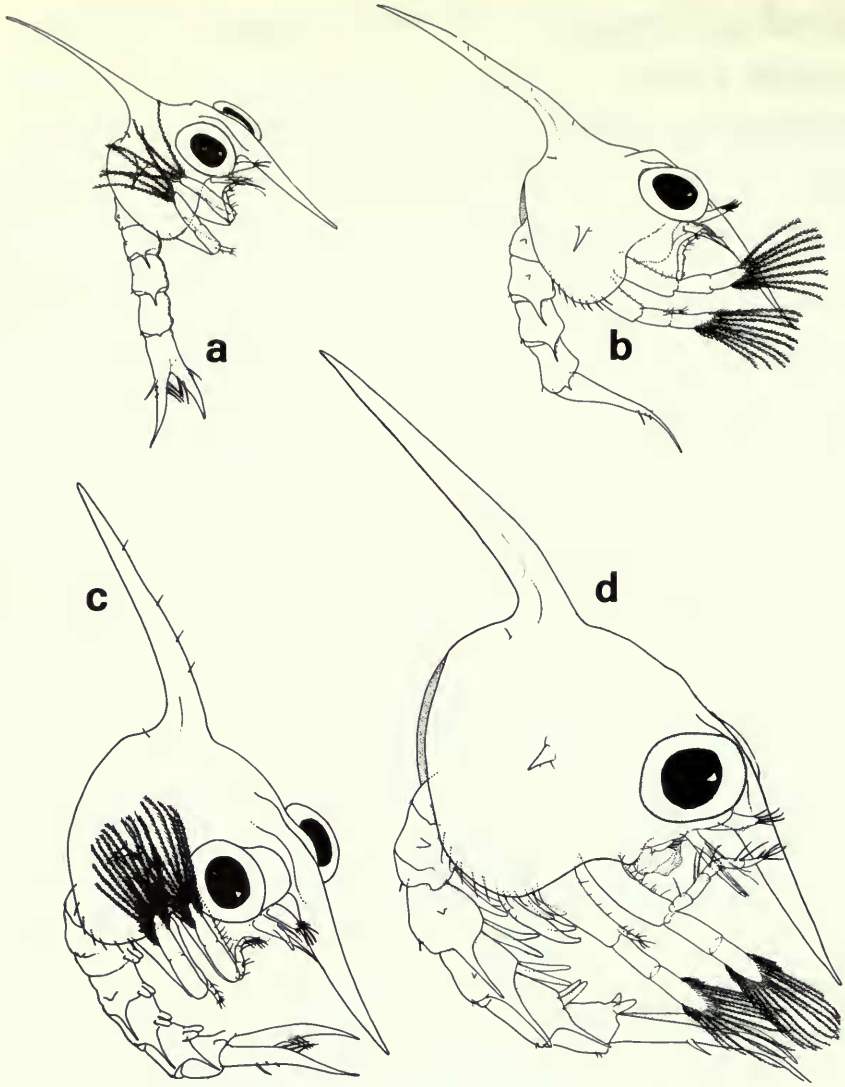

Fig. 1 *Geryon tridens*: zoeal stages (a) I, c.l. = 0·9 mm; (b) II, c.l. = 1·2 mm; (c) III, c.l. = 1·5 mm; (d) IV, c.l. = 2·0 mm.

specimen eighth, crab stage but further development was prevented by a failure of the air conditioning system.

Successfully reared larvae hatched as free swimming zoeae. Attempts were made to rear prezoeae liberated during the initial stages of hatching, but only one succeeded in developing to first zoea.

Descriptions

Geryon tridens Kröyer, 1837

Larval references: *Geryon tridens* Brattegard & Sankarankutty, 1967 : 7–12, figs 1–3 (prezoea, 1st zoea).

First zoea

DIMENSIONS. T.T. 2·6–2·8 mm; C.L. 0·8–0·9 mm.

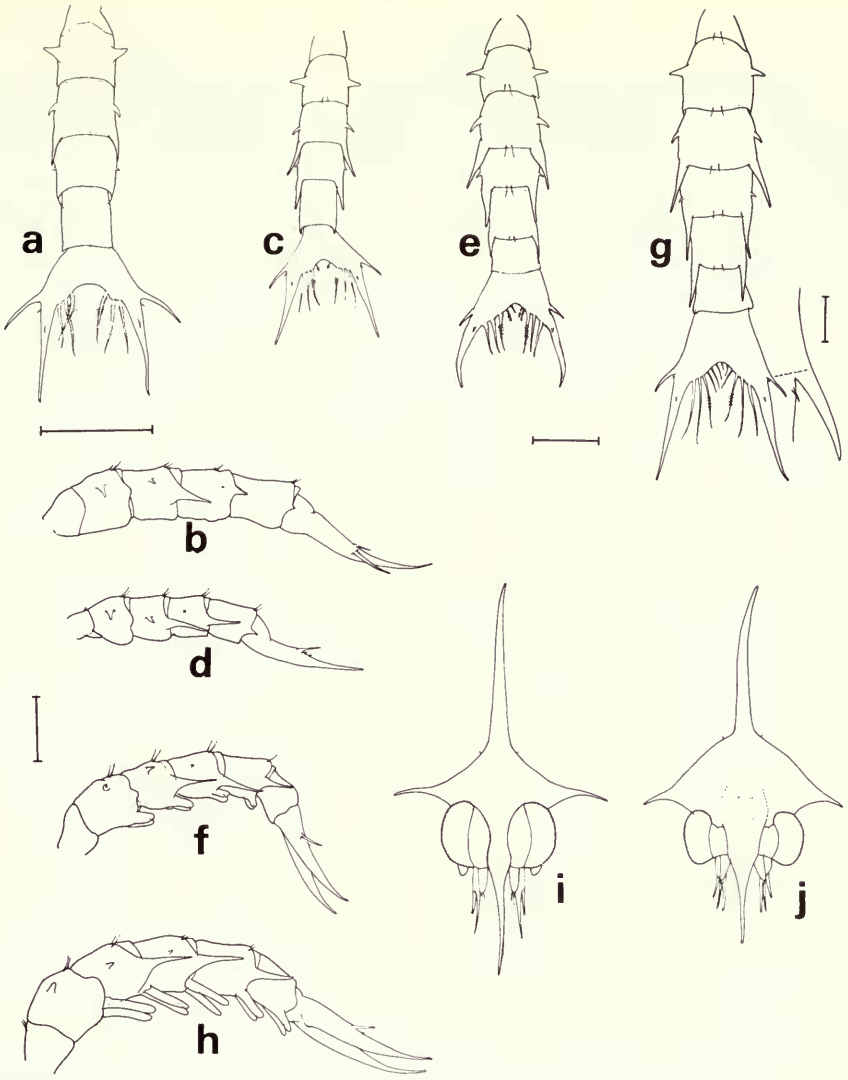

Fig. 2 *Geryon tridens*: abdomens of zoeal stages I–IV, dorsal (a), (c), (e), (g) and lateral (b), (d), (f), (h) aspects. Frontal aspects of (i) zoea I, (j) zoea IV. Scale = 0·5 mm, inset of (g) = 0·1 mm.

CARAPACE (Figs 1a, 2i). Dorsal spine well developed, straight, narrowing distally. Rostral spine straight, lateral spines long. Dorso-median elevation prominent. A pair of small dorso-lateral setae near base of dorsal spine. Posterio-lateral margin of carapace with a row of short spinules.

EYES. Partly fused to carapace.

ANTENNULE (Fig. 3a). Unsegmented, with two terminal aesthetascs and two short setae.

ANTENNA (Fig. 3f). Distal $\frac{1}{2}$–$\frac{2}{3}$ of spinous process spinulate; exopod not reaching into distal half of spinous process, with 2 terminal spines; endopod not developed.

MANDIBLE (Fig. 3k). Incisor and molar processes well developed, palp absent.

MAXILLULE (Fig. 4a). Endopod 2-segmented with 1, 6 setae respectively; basal endite with 4 setose spines and 2 setae; coxal endite with 9 setae.

MAXILLA (Fig. 5a). Endopod with large outer and small inner lobe with 5+3 setae; basal

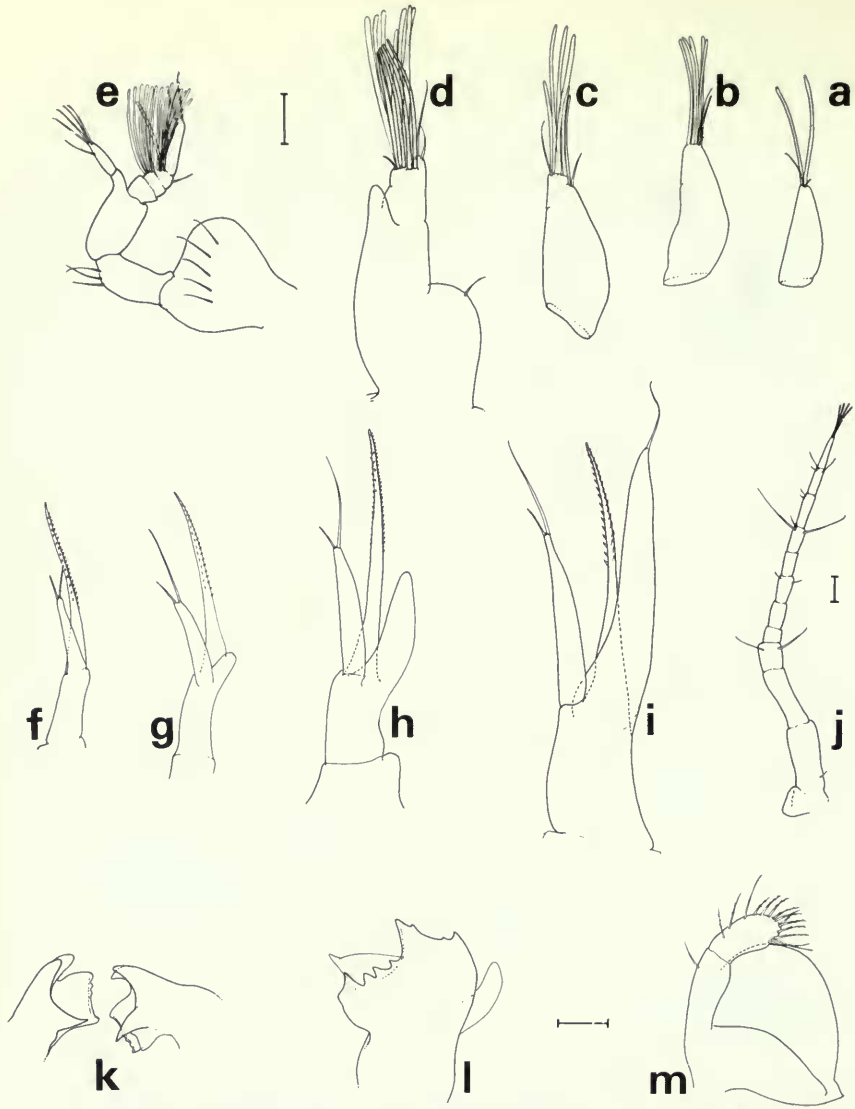

Fig. 3 *Geryon tridens*: antennules (a)–(d) of zoeae I–IV and (e) of megalopa. Antennae (f)–(i) of zoeae I–IV and (j) of megalopa. Mandibles (k) of zoeae I, (l) of zoea IV from ventral aspect and (m) of megalopa from dorsal aspect. Scales = 0·1 mm.

endite with large outer and small inner lobe with 6+5 setae; coxal endite bilobed with 4+3 setae; scaphognathite with 8 marginal setae and one long plumose posterior projection.

First maxilliped (Fig. 6a). Basis with 9–10 setae (arranged 2, 2, 3, 3); endopod 5-segmented with 2, 2, 1, 2, 4+1 setae; exopod incipiently 2-segmented with 4 terminal natatory setae.

Second maxilliped (Fig. 7a). Basis with 4 setae; endopod 3-segmented with 1, 1, 5 setae; exopod incipiently 2-segmented with 4 terminal natatory setae.

Third maxilliped and pereiopods. Represented as unsegmented buds.

Abdomen (Fig. 2a, b). 5-segmented+telson; 2nd segment with a pair of outwardly directed dorso-lateral processes; 3rd segment with a pair of smaller posteriorly curved dorso-lateral processes; 4th segment with a small pair of dorso-lateral spines. Posterio-lateral processes of

3rd to 5th segments decreasing in size on successive segments. A pair of minute setae near posterio-dorsal margin of each segment. Telson forks long, diverging posteriorly, with one long and one small lateral spine, dorsal spine well developed. Inner posterior margin of telson convex and with 3 pairs of long setae, innermost pair with long setules in middle section.

Second zoea

DIMENSIONS. T.T. 3·4–3·6 mm; C.L. 1·2–1·3 mm.

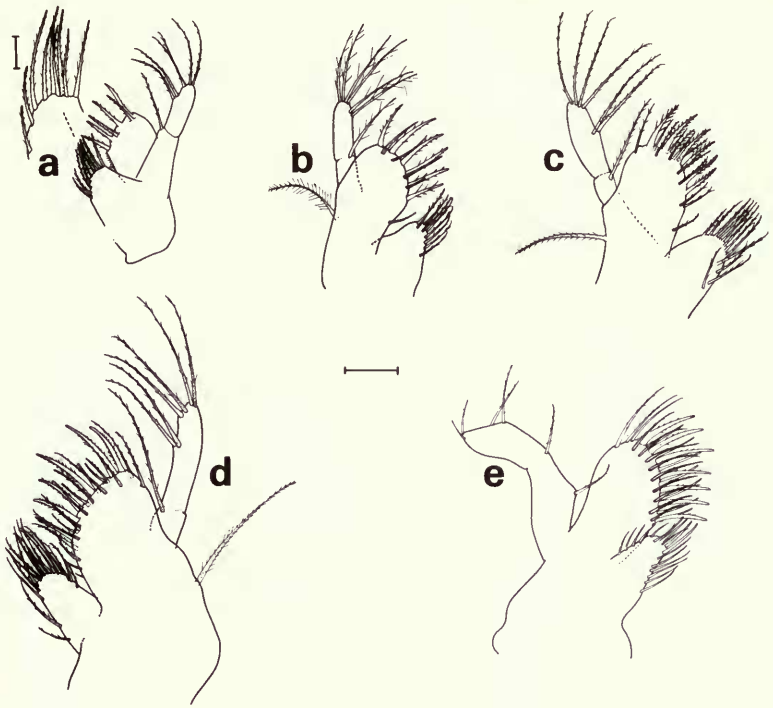

Fig. 4 *Geryon tridens*: maxillules (a)–(d) of zoeae I–IV and (e) of megalopa. Scale = 0·1 mm, inset to (a) = 0·03 mm.

CARAPACE (Fig. 1b). Considerably elevated in cross-section; dorsal spine sometimes with minute spinules; posterio-lateral margin with much longer spinules than in first stage.

EYES. Now stalked.

ANTENNULE (Fig. 3b). With 6 aesthetascs.

ANTENNA (Fig. 3g). Longer of the terminal spines on exopod much longer than in first stage: endopod bud well developed.

MANDIBLE. Unchanged.

MAXILLULE (Fig. 4b). Outer margin of basal endite with a prominent plumose seta, distal margin with 6 setose spines and 5 setae; coxal endite with 10–11 setae.

MAXILLA (Fig. 5b). Basal endite with 7+7 setae; coxal endite with 4+4 setae; scaphognathite with 18 marginal setae.

FIRST MAXILLIPED (Fig. 6b). Exopod with 9–10 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7b). Distal segment of endopod with 6 setae; exopod with 9–10 terminal natatory setae.

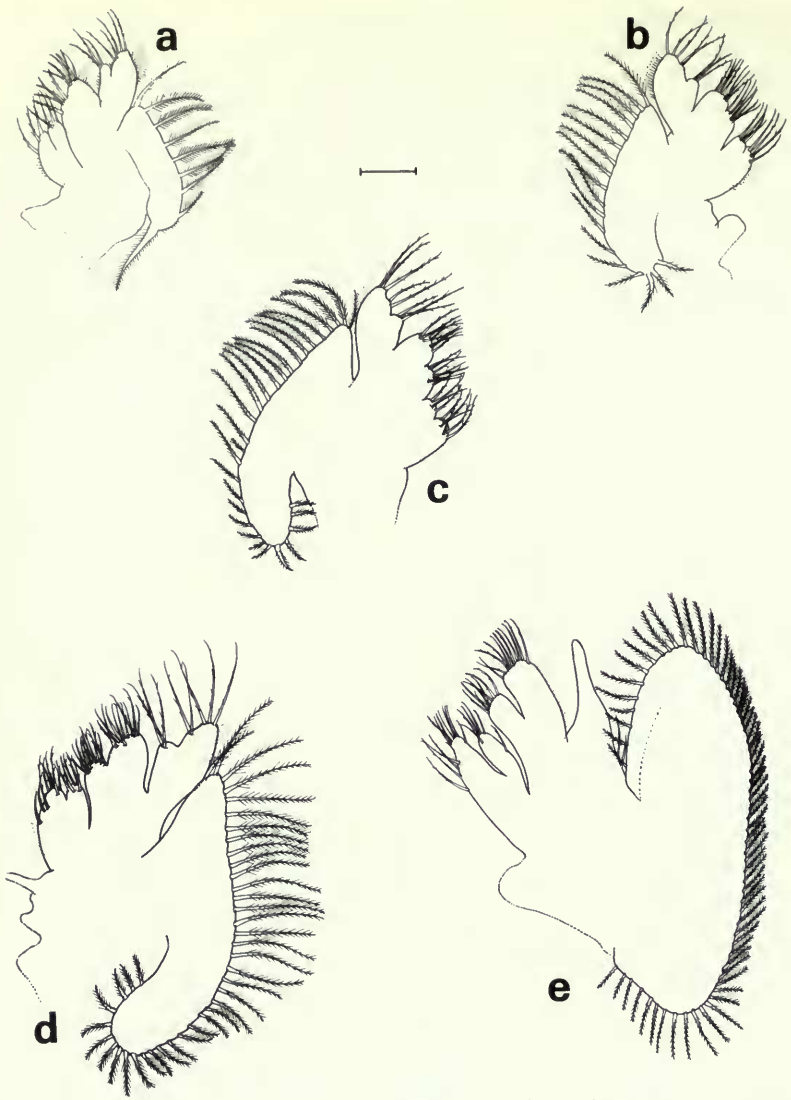

Fig. 5 *Geryon tridens*: maxillae (a)–(d) of zoeae I–IV and (e) of megalopa. Scale = 0·1 mm.

THIRD MAXILLIPED AND PEREIOPODS. Unsegmented buds larger than those of first stage.

ABDOMEN (Fig. 2c, d). Posterio-lateral processes longer than those in first stage. Inner margin of telson with 4 pairs of setae, innermost pair small.

Third zoea

DIMENSIONS. T.T. 4·0–4·2 mm; C.L. 1·5–1·6 mm.

CARAPACE (Fig. 1c). Dorsal spine stouter than in 2nd stage; setules prominent when present.

EYES Unchanged.

ANTENNULE (Fig. 3c). Setation unchanged.

ANTENNA (Fig. 3h). Exopod reaching into distal half of spinous process; endopod bud much longer than in 2nd stage.

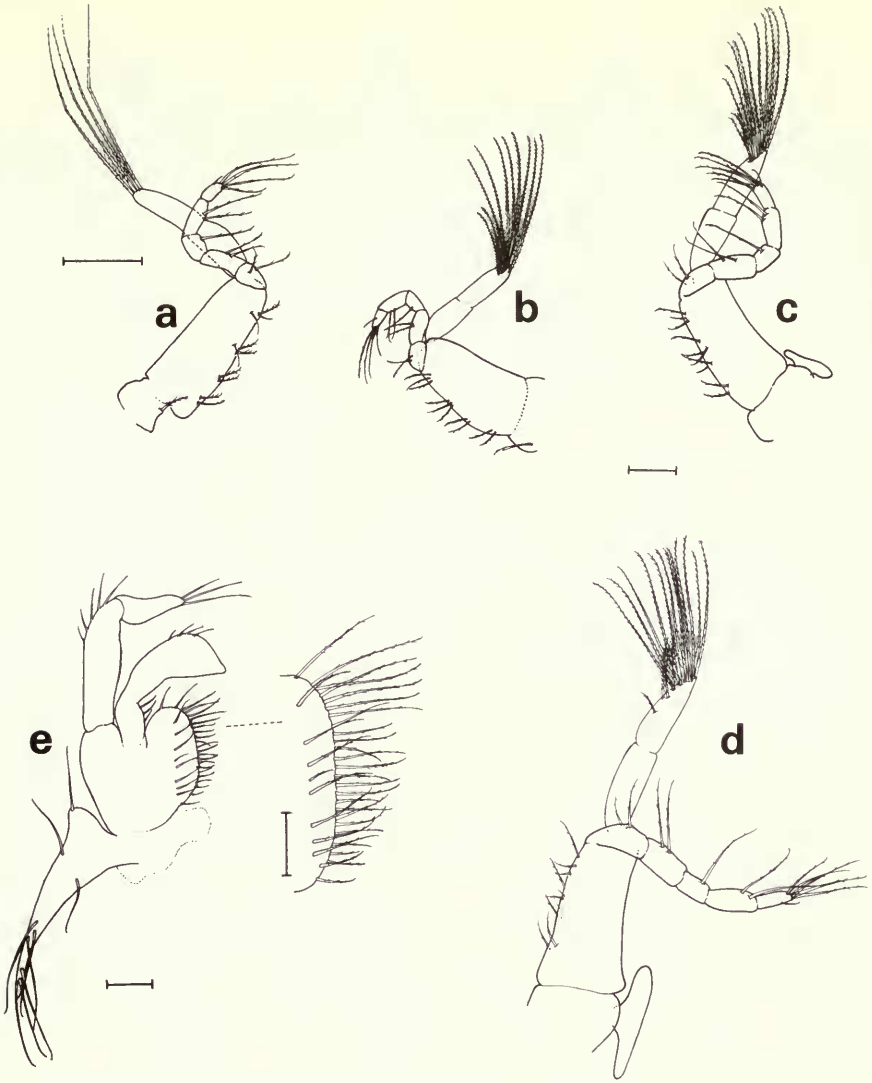

Fig. 6 *Geryon tridens*: 1st maxilipeds of (a)–(d) zoeae I–IV and (e) of megalopa. Scales = 0·2 mm except inset to (e) = 0·1 mm.

MANDIBLE. Incisor and molar processes broader and serrate.

MAXILLULE (Fig. 4c). Basal endite with 12 setae; coxal endite with 12–13 setae.

MAXILLA (Fig. 5c). Basal endite with 8+8 setae; coxal endite with 4+6 setae; scaphognathite with 25–29 setae.

FIRST MAXILLIPED (Fig. 6c). Coxa with prominent epipod; endopod distal segment with 5+1 setae; exopod with 12–14 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7c). Coxa with epipod; exopod with 12–14 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS. Buds larger than those of 2nd stage.

ABDOMEN (Fig. 2e, f). 6-segmented; posterio-lateral processes, particularly of 4th–5th segments, longer than in 2nd stage. Pleopod buds developed, vestigial on 6th segment. Inner margin of telson with 5 pairs of setae (but sometimes with 6 setae on one side and 5 on other).

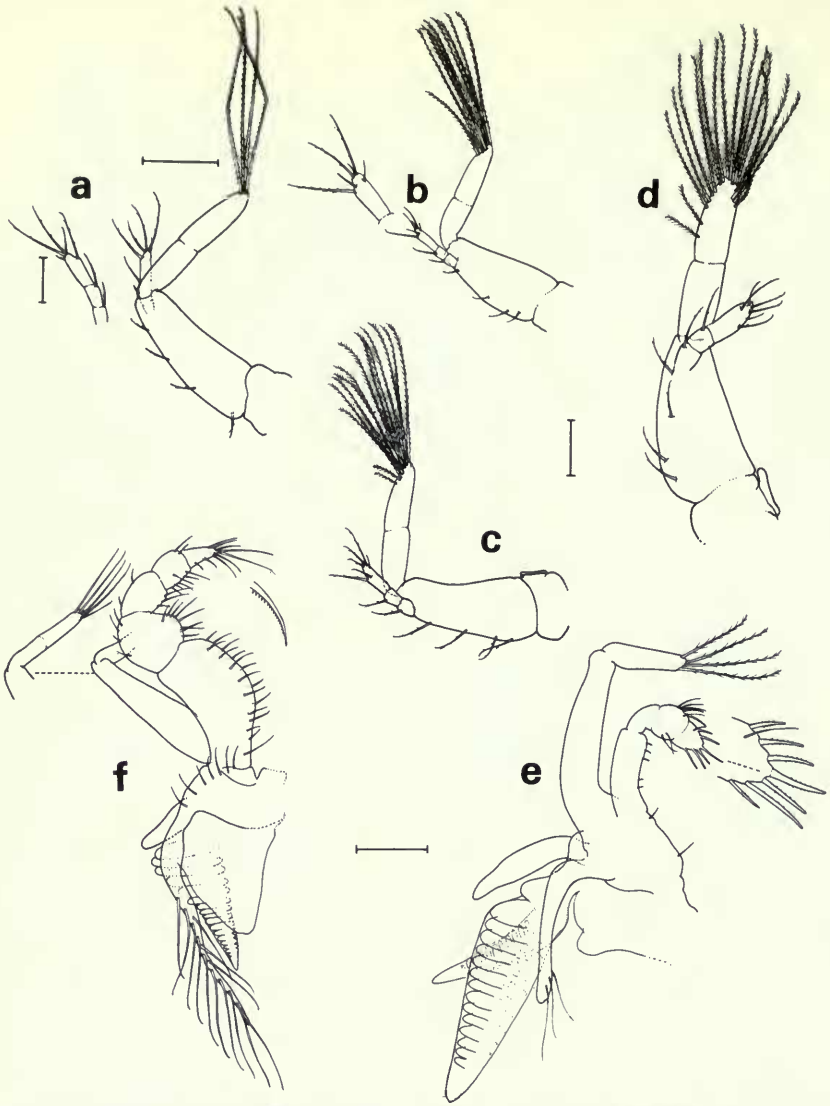

Fig. 7 *Geryon tridens*: 2nd maxillipeds of (a)–(d) zoeae I–IV and (e) of megalopa; (f) 3rd maxilliped of megalopa. Scales = 0·2 mm except insets to (a) and (b) = 0·1 mm.

Fourth zoea

DIMENSIONS. T.T. 4·9–5·2 mm; C.L. 1·8–2·0 mm.

CARAPACE (Figs 1d, 2j). Lateral spines slightly shorter than in 3rd stage.

EYES. Unchanged.

ANTENNULE (Fig. 3d). With 11 aesthetascs and 3 setae; endopod developed as a bud.

ANTENNA (Fig. 3i). Exopod reaching well into distal half of spinous process; endopod unsegmented, almost as long as spinous process and with a terminal seta.

MANDIBLE (Fig. 3l). With an unsegmented palp.

MAXILLULE (Fig. 4d). Basal endite with 18 setae; coxal endite with 17 setae.

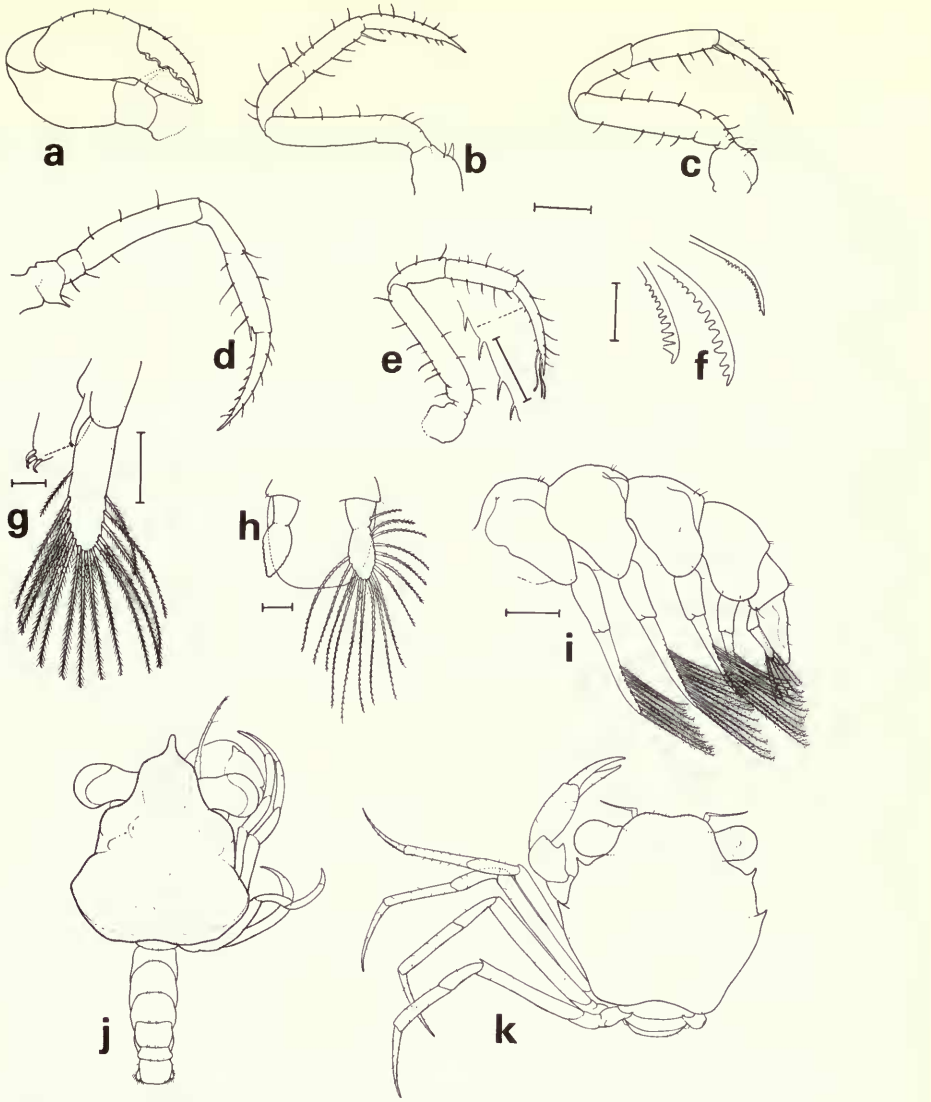

Fig. 8 *Geryon tridens*: megalopa (a)–(e) 1st to 5th pereiopods, scale = 0·5 mm, inset to (e) = 0·3 mm; (f) subterminal setae on dactylus of 5th pereiopod, scale = 0·05 mm; (g) 1st pleopod, scale = 0·3 mm, inset, scale = 0·05 mm; (h) telson and uropods, ventral aspect, scale = 0·1 mm; (i) abdomen, lateral aspect, scale = 0·5 mm; dorsal aspects of (j) megalopa c.l. = 3·0 mm and (k) 1st crab stage c.l. = 3·0 mm.

MAXILLA (Fig. 5d). Basal endite with 11 + 10 setae; coxal endite with 5 + 8 setae; scaphognathite with 40–42 setae.

FIRST MAXILLIPED (Fig. 6d). Coxal epipod longer than in 3rd stage; exopod with 16–17 terminal natatory setae.

SECOND MAXILLIPED (Fig. 7d). Coxal epipod larger than in 3rd stage; exopod with 17–18 terminal natatory setae.

THIRD MAXILLIPEDS. With a well developed exopod and 2 gill buds.

PEREIOPODS. Incipiently segmented, first pair chelate.

ABDOMEN (Fig. 2g, h). Smaller of 2 lateral spines on telson very reduced. Pleopod buds longer than in 3rd stage. Inner margin of telson with 6 pairs of setae.

Megalopa

DIMENSIONS. C.L. 3·0–3·1 mm.

CARAPACE (Fig. 8j) Longer than broad, narrowing anteriorly. Frontal region with a deep median furrow, rostrum deflected ventrally; each protogastric and inner epibranchial region with a small swelling; mesogastric region depressed; cardiac with a narrow and a broad U-shaped carina and one anteriorly placed tubercle on either side; intestinal region with a minute median tubercle.

EYES. Large and long, with well-developed cornea.

ANTENNULE (Fig. 3e). Peduncle 3-segmented, 1st segment with a row of transversely placed setae; 2nd segment with 3 disto-internal setae; exopod 4-segmented, 2nd segment with 6, 3rd with 10 aesthetascs and 2 setae respectively, 4th segment with 2 terminal setae; endopod segment with 4 terminal and 1 sub-terminal setae.

ANTENNA (Fig. 3j). Peduncle 3-segmented, 3rd segment with 2 long setae, flagellum 8-segmented, 3rd segment with 2 setae, 5th segment with 2 long and 1 short setae, 6th–7th segments with 2 and 3 setae respectively, 8th segment with 4 terminal aesthetascs.

MANDIBLE (Fig. 3m). Incisor process expanded as a broad concave plate with a sharp curved margin, molar process reduced; mandibular palp stout 2-segmented, proximal segment longer than distal with 1 disto-external setae, distal segment with 13–15 setae.

MAXILLULE (Fig. 4e). Endopod reduced but still with 6 setae; basal endite with 14 spines and 12–13 setae; coxal endite still with 17 setae.

MAXILLA (Fig. 5e). Endopod reduced, at the most with 2 outer basal setae; basal endite with 11+8 setae; coxal endite with 6+13–14 setae; scaphognathite with 62–63 setae.

FIRST MAXILLIPED (Fig. 6e). Exopod 2-segmented, proximal segment with 5 disto-external setae, distal segment with 3 terminal setae; basis with a longitudinal row of 23–25 marginal setae and a further row of 8–9 setae near inner margin of ventral surface; endopod indistinctly 2-segmented, terminally sub-acute with 3 setae on inner proximal margin and 4 setae on disto-outer margin; epipod well developed and with 10–12 setae.

SECOND MAXILLIPED (Fig. 7e). Coxa with 2–3 setae on inner margin; endopod 4-segmented, basal segment (merus) longest and with 5 small marginal setae, 3rd segment (propodus) with 2 spines and 6 setae, 4th segment (dactylus) with 7 spines and 1 seta; exopod 2-segmented, distal segment with 4 terminal setae; epipod bifurcate, longer and thinner part of bifurcation with several sub-terminal setae.

THIRD MAXILLIPED (Fig. 7f). Coxa/basis with a transverse row of setae; ischium inner margin with 17–25 setae, outer margin of merus with 3–4 setae, inner margin with 8–9 setae, carpal outer margin with 2 and inner with 3 setae respectively, propodal outer margin with 2 and inner with 7–8 setae, dactylus with 2 inner proximal and 7 terminal setae; exopod 3-segmented, distal segment with 5 terminal setae; epipod bifurcate, longer part setose.

PEREIOPODS (Figs 8a–e). Cheliped (a) stout and with a prominent ischio-basal spine; inner distal propodal margin and inner margin of dactylus with 3–4 blunt teeth. Pereiopods 2–5 (b–d) thin, inner margin of dactylus of each with 5–7 small spines, distal inner propodal margin with a spine, long on 2nd–3rd pereiopods; coxae of 2nd to 4th pereiopods each with a prominent spine, dactylus of 5th with 3 subterminal setae.

ABDOMEN (Figs 8i, j). With 6 segments+telson; posterio-lateral margins rounded and with 1–2 pairs of setae near dorso-lateral margin of each segment; telson slightly broader than long and

with 2 pairs of median setae. Five pairs of pleopods, exopod of each with 15 marginal plumose setae on distal segment, basal segment of 5th (uropod) with a seta on outer margin; endopods of pleopods 1–4 with 3 distally placed coupling hooks.

First crab stage

DIMENSIONS. C.L. 3·0–3·1 mm.

CARAPACE (Fig. 8k). Slightly longer than broad, frontal region with a longitudinal median furrow; antero-lateral margins each with 2 well-developed teeth.

PEREIOPODS (Fig. 8k). Cheliped moderately stout, carpal process acute. Pereiopods 2–5 long and thin, conspicuously setose.

Taxonomic remarks

The present laboratory reared material agrees with the account of the first zoea by Brattegard & Sankarankutty (1967) except in the following details.

	Brattegard & Sankarankutty	Present material
TOTAL LENGTH:	2·0 mm	2·6–2·8 mm
ABDOMEN:	? Without setae near posterio-dorsal margin of segments 1–5	with a pair of setae on posterio-dorsal margins of segments 1–5
ANTENNULE:	4 aesthetascs + 1 spinule	2 aesthetascs + 2 short setae
MANDIBLE:	? undifferentiated	a clearly differentiated molar and incisor
MAXILLULE:	basal endite with 6 (5 in fig.) 'strong setae'; coxal endite with 7 setae	basal endite with 4 spines and 2 setae; coxal endite with 9 setae
MAXILLA:	coxal endite with 10 setae; scaphognathite with 7 setae	coxal endite with 11 setae; scaphognathite with 8 setae

The complete larval development of only one other species of *Geryon* (the western Atlantic *G. quinquedens* Smith) has been previously described (Perkins, 1973). The zoeal stages of this species are noticably larger than those of *G. tridens* and dorso-lateral processes are usually developed on the fifth abdominal segment in *G. quinquedens*, whilst the pair on the fourth are much larger than the small spines on the corresponding segment of *G. tridens*. The posterio-lateral processes on the fifth segment of the abdomen are also much larger than those of *G. tridens*. The megalopa of *G. quinquedens* has only two subterminal setae on the dactylus of the fifth pereiopod compared with three present in *G. tridens*, and the exopods of the first to fifth pleopods are invested with 28 marginal setae whilst *G. tridens* has only 16. Further differences between the larvae of the two species are apparent when the setation of the appendages is compared as tabulated below.

	G. tridens	*G. quinquedens*
	First zoea	
ANTENNULE:	2 aesthetascs + 2 setae	4 aesthetascs + 1 seta
MAXILLULE:	coxal endite 9 setae	coxal endite 6 setae
MAXILLA:	basal endite 6 + 5 setae coxal endite 4 + 3 setae scaphognathite 8 setae	basal endite 5 + 5 setae coxal endite 3 + 3 setae scaphognathite 7 setae

	G. tridens	*G. quinquedens*
	Second zoea	
ANTENNULE:	6 aesthetascs	4 aesthetascs
MAXILLULE:	basal endite 6 spines + 5 setae	12 spinous setae
MAXILLA:	basal endite 7 + 7 setae scaphognathite 18 setae	basal endite 7 + 5 setae scaphognathite 22 setae
1ST MXPD:	basis 8 setae	basis 10 setae
2ND MXPD:	distal endopod segment 6 setae	distal endopod segment 4 setae
	Third zoea	
ANTENNULE:	6 aesthetascs + 2 setae	7 aesthetascs + 3 setae
MANDIBLE:	palp not developed	palp developed
MAXILLULE:	basal endite 6 spines + 12 setae coxal endite 12–13 setae	basal endite 17 spinous setae coxal endite 17 setae
MAXILLA:	basal endite 8 + 8 setae coxal endite 4 + 6 setae scaphognathite 25–29 setae	basal endite 7 + 5 setae coxal endite 5 + 9 setae scaphognathite 31 setae
	Fourth zoea	
ANTENNULE:	11 aesthetascs + 3 setae endopod bud not setose	12 aesthetascs + 2 setae endopod bud setose
MAXILLULE:	basal endite 6 spines + 18 setae	basal endite 22 spinous setae
MAXILLA:	basal endite 11 + 10 setae coxal endite 5 + 8 setae scaphognathite 40–42 setae	basal endite 12 + 9 setae coxal endite 5 + 9 setae scaphognathite 54 setae
2ND MXPD:	exopod 17–18 setae	exopod 19 setae
	Megalopa	
MAXILLULE:	endopod 6 setae basal endite 14 spines + 12–13 setae coxal endite 17 setae	endopod 4 setae basal endite 35 spinous setae coxal endite 25 setae
MAXILLA:	endopod 2 basal setae; no lateral setae basal endite 11 + 8 setae coxal endite 6 + 13–14 setae scaphognathite 62–63 setae	endopod 3 basal setae; 8 lateral + 1 proximal setae basal endite 14 + 11 setae coxal endite 8 + 16 setae scaphognathite 100 setae
1ST MXPD:	exopod, proximal segment 5 disto-external setae, terminal segment 3 setae basal endite 33–34 setae	exopod, proximal segment 6 disto-external setae, terminal segment 5 plumose setae basal endite 37 setae
2ND MXPD:	merus 5 marginal setae carpus without setae dactylus 7 spines + 1 setae proximal segment of exopod without setae	merus 3 marginal setae carpus 3 setae dactylus 10 setae (or spines) proximal segment of exopod with 4 marginal setae
3RD MXPD:	dactylus 9 setae exopod distal segment 5 setae	dactylus 12 setae exopod distal segment 6 setae

The zoeae of *G. tridens* can be readily distinguished from zoeae of all other brachyuran crabs reported from seas adjacent to the British Isles, except *Goneplax rhomboides* (Linnaeus), by the presence of dorso-lateral spines on the fourth segment of the abdomen. The features that separate *G. tridens* zoeae from those of *G. rhomboides* are tabulated below.

Zoeal features	*G. tridens*	*G. rhomboides* (after Lebour, 1928; Bourdillon-Casanova, 1960; Rice & Williamson, 1977)
Posterio-lateral margin of carapace:	with short spinules	with teeth and setae
Margins of posterio-lateral process of abdominal segments	unarmed	denticulate (see Bourdillon-Casanova, fig. 57a)
Telson forks:	unarmed two lateral spines on each fork in ZI–III	with minute spinules one lateral spine on each fork in all stages
Antennal exopod:	noticeably shorter than spinous process in early stages	almost, or as long as spinous process in early stages, shorter in later stages
Maxilla of ZIII:	scaphognathite with 25–29 setae	scaphognathite with 18–19 setae
1st maxilliped		
endopod setae of ZIII	2, 2, 1, 5+1	3, 2, 1, 2, 5,
exopod setae of ZI–IV	4, 9–10, 12–14, 17–18	4, 6, 8, 9–10
2nd maxilliped		
endopod setae of ZIII	1, 1, 6	1, 1, 5
exopod setae of ZI–IV	4, 9–10, 12–14, 16–17	4, 6–7, 8–9, 9–11

Megalopal features	*G. tridens*	*G. rhomboides*
Rostrum:	pointed	truncate
Carapace:	unarmed	with a pair of short protogastric spines

The large number (16) of marginal uropod setae distinguish the megalopa of *G. tridens* from those belonging to the genera *Polybius* (10 setae), *Macropipus* (8–10 setae), *Carcinus* (5 setae), *Xaiva* (10 setae) and *Portumnus* (7 setae). In addition, the dactylus of the 5th pereiopod is styliform in *G. tridens* but conspicuously lanceolate in megalopae of *Polybius*, *Macropipus* and *Portumnus*.

Juveniles of the deep water species *Geryon affinis* Milne Edwards & Bouvier have been occasionally misidentified as *G. tridens*. The dactyli of pereiopods 2–5 of *G. tridens* are strongly dorso-ventrally flattened whereas they are laterally compressed in *G. affinis*. This dorso-ventral flattening is apparent in *G. tridens* from the third crab stage (c.l. 5·0 mm) onwards, and may provide a means for separating the early post-larval stages of both species when corresponding stages of *G. affinis* become available for comparison.

The N. Atlantic *G. tridens* is replaced southward by the closely related *G. longipes* A. Milne Edwards. The larval stages of this species are unknown although the first zoeal stage of '*Bathynectes* sp. A' figured by Rice & Williamson (1977 : 47, fig. 22 a–d) is almost certainly a *Geryon* zoea and may be *G. longipes*. At present adults of both species can be separated only by differences in relative lengths of pereiopods 2–5 and by the degree of development of the antero-lateral

carapace spines. In *G. tridens* the pereiopods are shorter and slightly stouter than those of *G. longipes* and the fifth is much less than twice the median length of the carapace. The antero-lateral carapace spines are also shorter, less spinose, and usually directed slightly more anteriorly than those of *G. longipes*. A comparison of the smallest juvenile of *G. longipes* (c.l. 17 mm, from the syntype series) with the largest reared crab of *G. tridens* (eighth stage c.l. 9·9 mm) has revealed that the limb/carapace ratios are the same for both species. However, the juvenile of *G. longipes* has the posterior pair of antero-lateral spines directed outward and set at an angle of a little less than 90° to the median axis of the carapace, whilst the corresponding pair of spines in *G. tridens* are directed forward as in the adult.

Brachyuran zoeae hitherto described from British waters, with few exceptions (*Ebalia*, Lebour, 1928 : 478; *Corystes*, Ingle & Rice, 1971 : 282), show regular increases of marginal setae on the exopods of the first and second maxillipeds (e.g. ZI 4 setae, ZII 6, ZIII 8, ZIV 10 and ZV 12 setae, respectively). The zoeae of *G. tridens* do not conform to this pattern as laboratory reared material show the following succession of setal development and variation — ZII 9–10 setae, ZIII 12–14, ZIV 16–18 setae. Irregular developmental sequences of exopod setae are, however, not unusual and occur in zoeae of the western Atlantic *G. quinquedens* and in some portunids (*Callinectes sapidus*, Costlow & Bookhout, 1959 and *Ovalipes ocellatus*, Costlow & Bookhout, 1966). In these species the exopod setal formulae differ sufficiently on either one pair, or on both pairs of maxillipeds, from one moult to the next to enable recognition of the individual zoeal stages.

Phylogenetic relationships

The larvae of *G. tridens* possess many portunid features (family Portunidae). In particular, the zoeae have long, relatively non-spinulate rostral and dorsal spines, outwardly directed long lateral carapace spines, a well-developed antennal exopod that is shorter than the spinous process, well-developed dorso-lateral processes on abdominal segments 2–3, a telson with three spinules on each fork (with the smallest one becoming reduced in later stages), the first maxilliped with two setae on the endopod first segment and the distal setae on the endopod of the maxilla arranged in three distinct groups.

Larval characters separating the three subfamilies of the Portunidae represented in British waters were given by Rice & Ingle (1975*a* : 148–149). Although the larvae of *G. tridens* do not possess all the characters listed for any one of these three subfamilies they show, nevertheless, strong affinities to the Polybiinae. The zoeae have the third segment of the endopod of the first maxilliped armed with a seta and well-developed lateral spines on the carapace, whilst the megalopa is without sternal cornuae, but has coxal spines on pereiopods 2–4 with a downward pointing rostrum, and the dorsal surface of the carapace is without spines or conspicuous processes.

Zoeae belonging to the Portunidae have dorso-lateral processes on abdominal segments 2–3, although they may disappear from the third segment in later stages; only exceptionally are these processes present on segments 4–5 (e.g. *Ovalipes*, Costlow & Bookhout, 1966, fig. 1a). These dorso-lateral processes are frequently well developed on the posterior abdominal segments of zoeae belonging to the families Xanthidae (e.g. *Menippe*, Porter, 1960, fig. 2u; *Panopeus*, Lebour, 1944, fig. 9 and *Eriphia*, Bourdillon-Casanova, 1960, fig. 55), the Goneplacidae (e.g. *Goneplax*, Lebour, 1928, Pl. XI, fig. 10; XII, fig. 1) and Grapsidae (*Plagusia*, Aikawa, 1937, fig. 35). The zoeae of *Menippe* and of *Goneplax* also have long posterio-lateral abdominal spines.

The zoeae of *G. tridens* possess a small but conspicuous pair of dorso-lateral processes on the fourth abdominal segment and, in later stages, the posterio-lateral spines are well developed on the second to fourth segment. In both features *G. tridens* shows affinities to the Xanthidae and Goneplacidae, whilst the first crab stage strongly resembles juveniles of the Goneplacidae (e.g. perhaps *Homoioplax* and *Psopheticus*) in having a sub-quadrate carapace with two antero-lateral teeth and long thin pereiopods, features that are not typical of the early post-larval stages of either xanthids or portunids.

The genus *Geryon* was assigned to the family Goneplacidae by Rathbun (1937 : 265), Sakai

(1939 : 554–555) and by Barnard (1950 : 282), but Bouvier (1940 : 261) placed in into the family Xanthidae. Colosi (1924), however, had already established the family Geryonidae for *Geryon* Kröyer, 1837 and the fossil genus *Archaeogeryon*. Balss (1957 : 1654) placed the Geryonidae between the Xanthidae and Goneplacidae. Boyden (1943) demonstrated serological affinities between *Geryon quinquedens* and a species of the family Xanthidae (*Menippe*) and Leone (1951) between species of Xanthidae and Portunidae (*Macropipus puber*), but these authors were not able to compare it with species in the Goneplacidae. Perkins (1973) also suggested that the larvae of *G. quinquedens* shared many features with those larvae in the family Xanthidae. The present study of the larval development of *G. tridens* supports this serological evidence and suggests that the Geryonidae may have been derived from the same phylogenetic stock as the Portunidae, Xanthidae and perhaps a part of the heterogenous Goneplacidae.

Acknowledgements

I wish to thank Mr K. Wilson and Mr M. Rolf of the MAFF Laboratory, Burnham-on-Crouch, for their generous assistance in obtaining the live *Geryon* female from which the larvae were reared, and Dr A. L. Rice, Institute of Oceanographic Sciences, for his comments on the manuscript.

References

Aikawa, H. 1937. Further notes on brachyuran larvae. *Rec. oceanogr. Wks Japan* **9** : 87–162.

Balss, H. 1957. *Decapoda . . . In: Dr H. G. Bronns Klassen und Ordnungen des Tierreichs. Fünfter Band*, I. Abteilung, 7. *Buch.*, **12** *Lief*; 1505–1672, Leipzig.

Barnard, K. H. 1950. Descriptive catalogue of South African Decapod Crustacea (Crabs and Shrimps). *Ann. S. Afr. Mus.* **38** : 1–837.

Bourdillon-Casanova, L. 1960. Le meroplancton du Golfe de Marseille: les larves de crustacés décapodes, *Recl. Trav. Sta. mar. Endoume* **30** : 1–286.

Bouvier, E. L. 1940. Décapodes Marcheurs. *Faune Fr.* **37** : 1–404.

Boyden, A. A. 1943. Serology and animal systematics. *Amer. Nat.* **77** : 234–255.

Brattegard, T. & Sankarankutty, C. 1967. On the prezoea and zoea of *Geryon tridens* Kröyer (Crustacea Decapoda). *Sarsia* **26** : 7–12.

Christiansen, M. E. 1969. *Marine invertebrates of Scandinavia, No. 2 Crustacea Decapoda Brachyura*, 143 pp. Universitetsforlaget, Oslo.

Colosi, G. 1924. Una specie fossile di Gerionide (Decapodi brachiuri). *Boll. Soc. Nat. Napoli* **35** (11) **15** : 248–255.

Costlow, J. D. Jr & Bookhout, C. G. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull. mar. biol. Lab. Woods Hole* **116** : 373–396.

—— —— 1966. The larval development of *Ovalipes ocellatus* (Herbst) under laboratory conditions. *J. Elisha Mitchell scient. Soc.* **82** : 160–171.

Ingle, R. W. & Clark, P. F. 1977. A laboratory module for rearing crab larvae. *Crustaceana* **32** : 220–222.

—— **& Rice, A. L.** 1971. The larval development of the masked crab, *Corystes cassivelaunus* (Pennant), reared in the laboratory. *Crustaceana* 20 : 271–284.

Kröyer, H. 1837. *Geryon tridens*, en ny Krabbe. *Naturh Tidsskr.* **1** : 15–21.

Lebour, M. V. 1928. The larval stages of the Plymouth Brachyura. *Proc. zool. Soc. Lond.* **2** : 473–560.

—— 1944. Larval crabs from Bermuda. *Zoologica* **29** : 113–128.

Leone, C. A. 1951. A serological analysis of the systematic relationship of the Brachyuran crab *Geryon quinquedens*. *Biol. Bull. mar. biol. Lab. Woods Hole* **100** : 44–48.

Perkins, H. C. 1973. The larval stages of the Deep Sea Red Crab *Geryon quinquedens* Smith, reared under laboratory conditions (Decapoda : Brachyrhyncha). *Fishery Bull. natn. ocean. atmos. Adm.* **71** : 69–82.

Porter, H. J. 1960. Zoeal stages of the Stone Crab, *Menippe mercenaria* Say. *Chesapeake Sci.* **1** : 168–177.

Rathbun, M. J. 1937. The oxystomatous and allied crabs of America. *Bull. U.S. natn. Mus.* **166** : i–vi, 1–278.

Rice, A. L. & Ingle, R. W. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** : 101–119.

—— —— 1975*a*. A comparative study of the larval morphology of the British Portunid crabs *Macropipus puber* (L.) and *M. holsatus* (Fabricius), with a discussion of generic and sub-familial larval characters within the Portunidae. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** : 121–151.

—— **& Williamson, D. I.** 1977. Planktonic stages of Crustacea Malacostraca from Atlantic Seamounts. "*Meteor*" *Forsch.-Ergebn.*, D, No. 26 : 28–64.

Sakai, T. 1939. *Studies on the crabs of Japan*. IV. *Brachygnatha, Brachyrhyncha*, pp. 365–741. Yokendo Ltd, Japan.

Steedman, H. F. (ed.) 1976. Zooplankton fixation and preservation. In: *Monographs on oceanographic methodology*, 350 pp. Paris.

Zariquiey Alvarez, R. 1968. Crustáceos Decápodos Ibéricos. *Investigacion pesq.* **32** : i–xi, 1–510.

Manuscript accepted for publication 2 June 1978